TRANSVERSE PATTERN OF VEGETATION ON AVALANCHE PATHS IN THE NORTHERN ROCKY MOUNTAINS, MONTANA

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ABSTRACT.— The pattern of vegetation on avalanche paths has usually been ascribed to the damage done by snowslides. In the northern Rocky Mountains the pattern of herbs, shrubs, and small trees appears to be more complex than could be accounted for by avalanche magnitude and frequency. The vegetation on one path in Montana illustrates that the topography of the path is a factor in the distribution of species. Three zones exist across avalanche paths: an inner zone of herbs and suffrutescent shrubs occupying a ravine, which is snow covered longer ian elsewhere; flanking zones of dense shrubs and trees with flexible stems; and an outer zone of less dense shrubs that is more xeric. The pattern of vegetation seems to be due to avalanche-related stress rather than damage.

Avalanche paths cut vertical swaths through the mature subalpine forests of the western United States. The paths harbor singular assemblages of plant species that are not found elsewhere in the region. Avalanche paths present a variety of ecological problems: they are isolates; they are frequently disturbed; and they contain special features of the physical environment. In this paper we present observations of vegetative patterns on avalanche paths. These observations illustrate that disturbance and stress (sensu Grime 1979) define portions of a continuum of environmental events.

The vegetation on avalanche paths has been discussed in terms of the frequency and magnitude of avalanche events. Ives et al. (1976) described a transverse pattern of tree species on avalanche paths in Colorado. They reported an inner zone of alpine plants or aspen (*Populus tremuloides*) and willow (*Salix* spp.), which they associated with small, frequent avalanches. This inner zone is bounded by a zone of destroyed mature trees with seedlings or saplings of conifers and aspen where avalanches are larger and less frequent. Carrara (1979), also working in Colorado, attributed a similar vegetative pattern to the timing of large and small avalanche events. He distinguished between wider and higher dry snow avalanches and more restricted wet snow slides.

In Washington Smith (1974) attributed the distribution of species on avalanche paths to a combination of avalanche events and moisture gradients. She described a detailed transverse pattern of shrub species. She concluded that the pattern was related to a moisture gradient, which in turn was determined by the frequency of avalanches. Cushman (1976) used multivariate analysis to study avalanche paths in Washington. She found that avalanche frequency could be associated with shrub and tree communities, but was not well associated with herb/shrub communities. She hypothesized that herbaceous species were distributed in response to soil conditions related to snow cover on the paths.

Butler (1979), examining a longitudinal pattern on avalanche paths in Montana, found that flexible-stemmed deciduous trees were more common higher on the paths, and conifers became more common on the less frequently impacted runout zone. He attributed the difference in shrub and herbaceous composition between sites of different aspect (NW/SE) to moisture availability.

On numerous avalanche paths in Montana we have observed that up to three distinct zones occur between the trim lines of the

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mature forest. Such paths experience a return interval of 3–5 yr (Schaerer 1972, Butler 1979, Butler and Malanson 1984a). An inner zone is dominated by large herbs and suffrutescent shrubs. The inner zone is usually confined to a ravine containing an intermittent stream. On smaller paths the inner zone may be absent. Flanking the inner zone on either side are bands of small deciduous trees and shrubs with flexible stems. The density of shrubs is high in this flanking zone and decreases into the third and outer zone of the path. The outer zone is characterized by a community similar to that of the flanking zone, but at lower density.

These observations indicate that the transverse patterns of vegetation are more complex than can be accounted for by a magnitude/frequency hypothesis. The following section presents field data describing the transverse pattern of one avalanche path, from which we argue that a hypothesis stating that magnitude and frequency of events directly control the transverse pattern of vegetation on avalanche paths should be rejected.

Observations

Site.— We chose a single path that has three zones. The path, located on the southern boundary of Glacier National Park, was chosen prior to our perception of the nature of the transverse pattern of the vegetation. It has two source areas at an elevation of about 1800 m. The runout zone, which crosses Shed 7 of the Burlington Northern railroad, is at 1250 m. Tree-ring analysis of conifers damaged by avalanching indicates that major avalanches occurred on this path in 1982, 1979, 1974, 1972, 1970?, 1963, 1957, 1954, 1950?, and 1948 (Butler and Malanson 1984a).

Sample.— With a different purpose in mind, we sampled the vegetation on the path using a forest fire fuel inventory method (Brown et al. 1982). We ran four transects across the path, each 50 m apart. We located a sample plot next to the central stream channel on each transect and at 25 and 50 m away from the stream on both sides. The locations of the sample plots are shown in Figure 1. The topography and the vegetation bands are asymmetrical. Four plots, three on the eastern side of the path, are in the outer zone. The four centrally located plots are in the inner zone. The remaining 12 plots represent the flanking zone.

The fuel inventory for each plot included a count of the deciduous tree or shrub stems in two 1.01 m^2 circular plots. The stems were counted by diameter classes of 0–.5, .5–1.0, 1.0–1.5, 1.5–2.0, 2–3, 3–5, and >5 cm. The percent foliar cover of trees and shrubs in each plot was estimated by two workers, from whose observations a mean was computed. Shrubs and trees were identified by species.

Herbs were sampled by weight only. Four 0.1794 m^2 rectangular plots were arranged at corners of a 2-m square. The plot with the most abundant herb component was selected, and the abundance of the herbs in the other three plots was estimated, by two workers, as a percentage of the first plot. The aboveground herbs from the first plot were then clipped, taken from the field, dried, and weighed. The herbs were not identified by species in these samples, but the presence of dominant herbs was noted.

Results

In the inner zone the plant community is characterized by suffrutescent shrubs and herbs (Table 1). *Heracleum lanatum* is the dominant herb; others include *Veratrum viride* and *Urtica dioica*. The shrub diversity and stem coverage is less than that in the other zones (Table 2). *Rubus parvifolius* is the dominant shrub, although *Cornus stolonifera* and *Populus tremuloides* saplings dominate one inner zone plot. The community of the inner zone occupies a topographic ravine along the stream. At the edge of the ravine the break in slope coincides with a sharp vegetative boundary.

In the flanking zone, shrub and tree species dominate. *Populus tremuloides*, *Acer glabrum*, *Alnus sinuata*, and *Amelanchier alnifolia* are most abundant (Table 2). Shrub diversity is highest in the flanking zone, with richness ranging from 4 to 9. Herb biomass is high, but relatively less important than in the inner zone. On some plots at the left side of the path the herb biomass is notably high

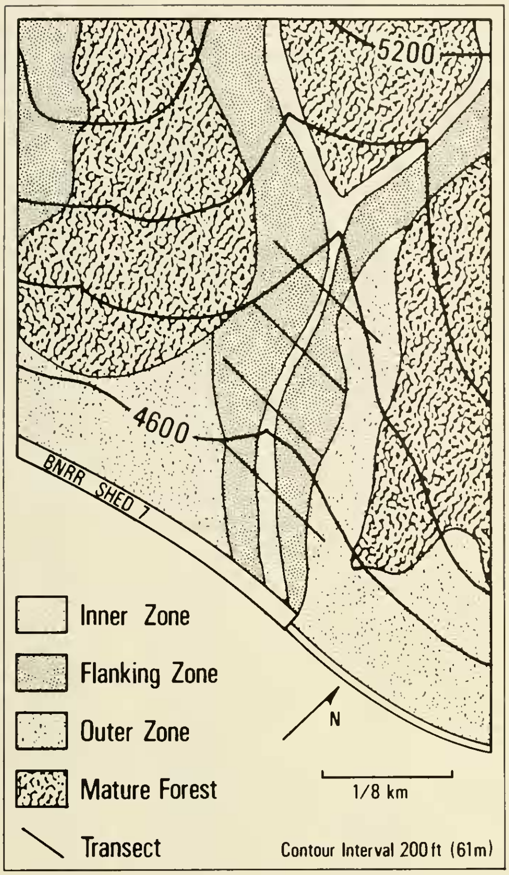

Fig. 1. Map of the vegetative patterns and sample transects on the avalanche path above Shed 7.

where the flanking zone is close to the forest margin (Table 1 and Fig. 1).

In the outer zone on the eastern side of the path shrub diversity, cover and stem density and size are low (Table 2). The biomass of herbs is also relatively low. This zone is comparatively depauperate in both biomass and species richness. It is generally farther from the stream and is open and exposed.

DISCUSSION

The pattern of vegetation we observed could not have resulted from differences in disturbance alone. The vegetation of the inner zone could be damaged by avalanches more frequently than vegetation in the flanking and outer zones; however, the vegetation in these exterior zones is well able to survive avalanche impact and burial. Further, little difference exists in shrub species composition between the flanking and outer zones. The avalanche factor most likely to influence the pattern of vegetation is burial by snow. Avalanches deposit large quantities of snow, even filling the topographic ravines of the inner zone (Butler 1984). The inner zone may remain under snow for several weeks after the rest of the path is clear. This shorter growing season is a stress (sensu Grime 1979), not a disturbance; growth is slowed, not destroyed. The primary factor is therefore topographic, not catastrophic.

From the edge of the inner ravine to the trimline of the path, a moisture gradient probably exists. The shrubs near the ravine should have access to a larger supply of soil moisture from the melting snow in the ravine and, later in the year, from the water table. The outer zone would have less accessible water, and, because it is more open, a more xeric microclimate. These views on available soil moisture are, at this time, necessarily speculative, but the differences in microclimate are obvious.

As noted above, some narrower avalanche paths lack a distinct inner zone. With less snow and less water, a deep ravine does not develop; the pattern of snow cover does not exist; and shrubs and trees are able to occupy the center of the path. In casual observations

TABLE 1. Biomass and foliar cover of herbs and shrubs on the plots in the inner (I), flanking (F), and outer (O) zones.

		Biomass (kg/m^2)		Cover (%)	
Plot	Zone	Herbs	Shrubs	Herbs	Shrubs
1	O	0.0250	0.5448	8	16
2	F	0.0773	9.4272	50	79
3	I	0.0463	1.5421	8	84
4	F	0.0477	8.4414	40	88
5	O	0.1065	0.8652	70	50
6	F	0.0584	12.4199	13	88
7	F	0.0522	10.1310	32	69
8	I	0.0820	4.6126	40	79
9	F	0.1194	3.0455	13	98
10	F	1.8729	0.8468	60	50
11	F	0.1071	8.4989	22	50
12	F	0.1023	0.8256	50	60
13	I	0.0923	1.1341	42	60
14	F	1.0080	7.3870	84	64
15	F	0.3463	2.1637	32	79
16	O	0.0777	0.4371	8	40
17	O	0.1384	0.7979	60	22
18	I	0.1260	0.4959	93	50
19	F	0.4817	1.2783	74	60
20	F	0.0687	9.6440	16	79

TABLE 2. Shrub stem area, stem density, and basal areas of the plots.

Plot	Species	Mean stem area (cm^2)	Stems/ Ha	Basal area/ Ha
1	*Amelanchier alnifolia*	.22	79,229	17,431
	Berberis repens	.14	44,567	6,175
2	*Amelanchier alnifolia*	.47	128,748	59,953
	Berberis repens	.05	24,759	1,238
	Populus tremuloides	7.50	14,856	11,402
	Prunus virginiana	.09	44,567	3,812
	Rosa spp.	.05	19,808	973
	Rubus idaeus	.05	34,663	1,702
	Vaccinium scoparium	.10	74,278	7,147
3	*Alnus sinuata*	.05	4,952	243
	Cornus stolonifera	.24	44,567	10,483
	Ribes lacustre	.20	9,904	1,945
	Rosa spp.	.36	34,663	12,589
	Rubus parviflorus	.44	14,856	6,563
	Vaccinium scoparium	.33	24,759	8,216
4	*Amelanchier alnifolia*	.44	4,952	2,188
	Populus tremuloides	9.62	14,856	142,927
	Prunus virginiana	.44	4,952	2,188
	Rhamnus alnifolia	.12	69,326	8,282
	Rosa spp.	.05	4,952	243
	Rubus parviflorus	.44	14,856	6,563
	Sorbus scopulina	2.90	14,856	43,011
	Vaccinium scoparium	.15	69,326	10,068
5	*Amelanchier alnifolia*	.61	19,808	12,047
	Berberis repens	.20	69,326	13,612
	Prunus virginiana	.51	44,567	22,587
	Rhamnus alnifolia	.79	9,904	7,779
	Rosa spp.	.05	4,952	243
	Rubus idaeus	.05	19,808	973
	Vaccinium scoparium	.14	29,711	4,117
6	*Arctostaphylos uva-ursi*	.05	9,901	486
	Berberis repens	.05	4,952	243
	Rubus ideaus	.05	44,567	2,188
	Rubus parviflorus	.05	4,952	243
	Spirea betulifolia	.34	138,651	47,435
	Vaccinium scoparium	.05	24,759	1,216
7	*Ceanothus* spp.	2.41	4,952	11,911
	Populus tremuloides	38.48	4,952	190,569
	Prunus virginiana	2.01	24,759	49,781
	Rosa spp.	.44	4,952	2,188
	Spirea betulifolia	.05	9,901	486
	Vaccinium scoparium	.44	19,808	8,751
8	*Cornus stolonifera*	.52	39,615	20,414
	Loncifera involuctra	1.00	19,808	19,864
	Populus tremuloides	2.24	19,808	44,431
	Rubus idaeus	.05	4,952	243
	Rubus parviflorus	.44	34,663	15,314
	Salix spp.	1.23	9,904	12,154
9	*Amelanchier alnifolia*	1.23	4,952	6,077
	Cornus stolonifera	1.43	24,759	35,440
	Rubus parviflorus	.24	24,759	5,883
	Sorbus scopulina	.88	9,904	8,740
	Vaccinium globulare	.28	99,037	28,002
10	*Amelanchier alnifolia*	.05	9,904	486
	Berberis repens	.05	4,952	243
	Prunus virginiana	.10	24,759	2,382
	Rosa spp.	.17	34,663	5,761
	Rubus parviflorus	.23	59,422	13,609
	Vaccinium globulare	.25	89,133	21,954

Table 2 continued.

Plot	Species	Mean stem area (cm^2)	Stems/ Ha	Basal area/ Ha
11	*Acer glabrum*	.08	123,796	9,344
	Amelanchier alnifolia	.49	54,470	26,700
	Arctostaphylos uva-ursi	.05	14,856	729
	Berberis repens	.05	9,904	486
	Populus tremuloides	3.98	24,759	98,444
	Prunus virginiana	.08	34,663	2,788
	Rubus idaeus	.05	118,844	5,834
	Vaccinium globulare	.05	4,952	243
	Vaccinium scoparium	.05	4,952	243
12	*Amelanchier alnifolia*	.26	44,567	11,775
	Pachistima myrsinites	.05	39,615	1,945
	Populus tremuloides	.44	4,952	2,188
	Prunus virginiana	.44	4,952	2,188
	Rosa spp.	.44	9,904	4,376
	Rubus idaeus	.05	99,037	4,862
	Spirea betulifolia	.14	29,711	4,117
	Vaccinium scoparium	.07	49,518	3,500
13	*Rubus parviflorus*	.29	183,219	53,545
14	*Acer glabrum*	2.81	44,567	125,032
	Amelanchier alnifolia	.28	49,518	14,001
	Berberis repens	.05	9,904	486
	Pachistima myrsinites	.05	4,952	243
	Rubus parviflorus	.24	24,759	5,883
	Spirea betulifolia	.08	44,567	3,364
15	*Acer glabrum*	.40	34,663	13,724
	Amelanchier alnifolia	1.23	9,904	12,154
	Pachistima myrsinites	.08	34,663	2,788
	Rubus parviflorus	.44	34,663	15,314
	Spirea betulifolia	.05	24,759	1,216
	Vaccinium globulare	.15	79,229	12,047
	Vaccinium scoparium	.26	44,567	11,775
16	*Amelanchier alnifolia*	.10	49,518	4,764
	Arctostaphylos uva-ursi	.06	128,748	7,372
	Berberis repens	.05	49,518	2,431
	Rubus idaeus	.05	49,518	2,431
	Vaccinium scoparium	.03	99,037	2,697
17	*Amelanchier alnifolia*	.41	79,229	32,258
	Berberis repens	.05	44,567	2,188
	Rosa spp.	.05	24,759	1,216
	Rubus idaeus	.05	69,326	3,403
	Vaccinium scoparium	.08	39,615	2,990
18	*Prunus virginiana*	.14	14,856	2,058
	Rosa spp.	.20	9,904	1,945
	Rubus parviflorus	.17	34,663	5,761
	Unidentified	.44	14,856	6,563
	Vaccinium scoparium	.29	54,470	14,919
19	*Amelanchier alnifolia*	.36	99,037	35,967
	Pachistima myrsinites	.10	99,037	9,529
	Rubus idaeus	.05	14,856	729
	Vaccinium scoparium	.20	9,904	1,945
20	*Alnus sinuata*	3.53	59,422	209,753
	Amelanchier alnifolia	.64	49,518	31,502
	Pachistima myrsinites	.11	19,808	2,247
	Rubus idaeus	.05	19,808	973
	Rubus parviflorus	.11	19,808	2,247
	Spirea betulifolia	.05	29,711	1,459
	Vaccinium globulare	.20	19,808	3,889

we detected considerable variation in the shapes and widths of the patterns. Although our data illustrate only one case, the topography of the paths seems more important than avalanche source areas in affecting the patterns.

Two areas of ecology have been separated in the recent literature: stress and disturbance (Cairns 1980, Barrett and Rosenberg 1981). We believe that, although some adaptations seem to be selected by either stress or disturbance, many environmental events have an effect that varies between stress and disturbance. The effect may depend on the intensity of the event. Following the definitions of stress and disturbance of Grime (1979), an event such as flooding may stress some species and damage others. Different flood events could damage all species or only stress all species (cf Malanson and Kay 1980, Menges and Waller 1983). Avalanche events also vary in intensity. The avalanches of Glacier National Park, Montana, and of the Cascades, Washington, are more often wet snowslides with lower velocities and impact pressures than would be found in the dry snow avalanches of Colorado and Utah. This difference may account for the simpler pattern described by Ives et al. (1976). Carrara (1979) thought that the pattern he observed was due to an older dry snow avalanche affecting the entire path, and a recent wet snow avalanche affecting only the inner zone. The difference in the location of wet and dry slides within a path may be of importance in Montana also (Butler and Malanson 1984b). In general, stress and disturbance in plant ecology can and should be integrated through an analysis of the environmental events.

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